

## MOLT, PLUMAGE ABRASION, AND COLOR CHANGE IN LAWRENCE'S GOLDFINCH

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**ABSTRACT.**—We examined molting, plumage abrasion, and seasonal color changes of Lawrence's Goldfinch, *Carduelis lawrencei*, to determine to what extent the reported brightening of male colors at the approach of the breeding season results from plumage renewal. Lawrence's Goldfinch has only one molt per year, a complete postbreeding prebasic molt. Color changes during spring result entirely from plumage abrasion and fading, not from a prealternate molt as previously was thought. The yellow breast feathers of the males, but not the females, are unusually resistant to wear, so that the yellow on the breast appears to expand and brighten, as less durable surrounding gray feathers abrade. This may be due to a one-third greater thickness of the rachillae of the yellow barbs in males, so that instead of the rachillae progressively losing yellow-pigmented material, the brown pigmented barbules break off, leaving intact the rest of the barb with only yellow pigment. In contrast, the yellow breast feathers of females abrade progressively at the tips of the rachillae. Females change dorsal coloration little, but males develop a yellowish area on the center of the back, which results when the olive to brown tips overlapping adjacent feathers wear off and uncover yellow proximal portions of neighboring feathers. We point out the need to examine plumage microscopically when studying molting and plumage changes so as not to reach false conclusions about the causes of the changes. Received 19 December 2001, accepted 20 July 2002.

As in many passerines, the male Lawrence's Goldfinch, *Carduelis lawrencei*, is more brightly and conspicuously colored than the female, especially during the breeding period (Davis 1999). The functions and evolution of such sexual dichromatism have interested investigators for a long time (Darwin 1874, Hamilton and Barth 1962, Butcher and Rohwer 1989, Savalli 1995). Some species, such as the American Goldfinch, *C. tristis*, increase sexual dichromatism before breeding by molting, whereas others, such as the Snow Bunting, *Plectrophenax nivalis*, do so by feather wear (Chapman 1939, Lyon and Montgomerie 1995). The expense of time, nutrients, and energy during molting probably imposes significant physiological and ecological constraints that must be accounted for in any analysis of the proximate and ultimate causes of sexual dichromatism (King 1980, Walsberg 1983, but see Brown and Bryant 1996).

Published descriptions of seasonal color changes in Lawrence's Goldfinch have been ambiguous. Some authors described the male Lawrence's Goldfinch as having a browner back and hindneck (nape) during autumn and winter, and getting an additional touch of yellow on the middle of the back during summer

(Dawson 1923, Edwards 1989, National Geographic Society 1999). Others described the back as being more extensively greenish yellow during winter (Clement et al. 1993), or infused with Spectrum Yellow extending from lower back to the nape during winter, but duller and browner than during summer (Davis 1999; color names that are capitalized are those of Smithe 1974, 1975, 1981). All authors noted that the yellow of the underparts appears more extensive during summer than during winter. The female is similar to the male without black on the head and throat, but duller overall (Dawson 1923) or with a smaller, duller yellow patch on her breast (Davis 1999).

It appears that these color changes result from a body molt during spring, since Lawrence's Goldfinch is reported to undergo a "limited-partial" prealternate molt (Pyle et al. 1997), or an extensive prealternate molt involving all the body feathers (Davis 1999) during March and April. However, in this study we present evidence that color change results instead from feather wear. To characterize the extent and origins of seasonal color change, we quantified the changes of color between winter and summer, and the molting and plumage abrasion throughout the year.

### METHODS

*Molt and plumage wear.*—To determine when molting occurs, one of us (EJW) examined 190 study skins

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TABLE 1. Criteria for determining the molt score of a passerine study skin.

Areas scored	Score	Criteria
Chin, throat, and breast	0	No feathers in any stage of growth are present.
	1	One or more feathers growing on one side only.
	1	One or two feathers growing on the midline.
	2	Three to five feathers growing on or across the midline.
	3	Six or more feathers growing on or across the midline.
Sides and face	0	No feathers in any stage of growth are present.
	1	One or more feathers growing on one side only.
	2	One to five feathers growing on each side.
	2.5	One to five feathers growing on one side, but six or more growing on the other.
	3	Six or more feathers growing on each side.
Crown, back, and rump	0	No feathers in any stage of growth present.
	1	One or more feathers growing on one side only.
	1	One or more feathers growing on the midline.
	2	Three to five feathers growing on or across the midline.
	3	Six or more feathers growing on or across the midline.
Primaries, secondaries	0	No feathers in any stage of growth present.
	1	One or more growing on one wing only.
	2	One or two growing on each wing.
	2.5	One or two growing on one wing, three or more growing on the other.
	3	Three or more growing on each wing.
Rectrices	0	None growing.
	1	One or more growing on one side only.
	2	One or two growing on each side of midline (e.g., 1-1, or 2-2, or left 1 and 3-3, etc.).
	3	Three or more growing on each side.

(see acknowledgments for sources) collected at all times of the year. These specimens had been collected over many years between 1858 and 1972, and represent conditions during a typical calendar year. All but 11 specimens were from the combined breeding and wintering range in California and northern Baja California. The rest were collected during October through December in the extension of the wintering range into Clark County, Nevada, and southern Arizona. We classified specimens according to age characteristics of plumage as HY (in calendar year of hatching), AHY (in second or subsequent calendar year), or U (undetermined age; HY birds that had had a complete first prebasic molt could not be distinguished from older birds; Pyle *et al.* 1987, 1997). EJW scored molting by examining each specimen under a 7× dissecting microscope, lifting feathers with a dissecting needle to examine their bases and surrounding skin for presence of basal sheaths, pinfeathers, and intermediate stages

of feather growth (Willoughby 1986, Willoughby 1991). He counted all feathers in any stage of active growth, assigning scores of 0, 1, 2, and 3 according to criteria in Table 1 to each of these plumage areas: (1) chin and throat—feathers of the interramal, submalar, and anterior two thirds of the cervical regions of the ventral tract; (2) breast—feathers of the posterior one third of the cervical and anterior one third of the sternal regions of the ventral tract; (3) sides—feathers of the abdominal and posterior two thirds of the sternal regions of the ventral tract; (4) face—feathers of the malar, auricular, post-auricular, loreal, superciliary, and ocular regions of the capital tract; (5) crown, including forehead, pileum, and occiput, (6) back and rump—feathers of interscapular, dorsal, and pelvic regions of the spinal tract; (7) primaries, (8) secondaries, and (9) rectrices. Adding the scores of all areas yielded a total score for each specimen from 0 (no molting anywhere) to 27 (substantial molting everywhere). This score cor-

related strongly ( $r = 0.98$ ) with the total number of growing feathers on the specimen raised to the power 0.67. The relationship was described by the equation:

$$\text{Number of growing feathers} = (1.127 y)^{1.493},$$

where  $y$  = molt score. This equation is derived from molt scores and counts of growing feathers of 170 study skins of male American Goldfinches of all ages (EJW unpubl. data). To document patterns of wing and tail replacement, we scored flight feather molt by the method of Newton (1966).

EJW scored each specimen for wear by the method of Willoughby (1986, 1991). Body feathers scored 0 (no wear) when little or no wear was evident, 1 (light wear) when at least one barb lacked up to 1/3 of its original length, 2 (moderate wear) when two or more barbs lacked 1/3 to 2/3 of their original lengths, and 3 (heavy wear) when two or more barbs lacked more than 2/3 of their original lengths. Each plumage area, except face and sides, received the score of the most highly worn 25% or more of the feathers present, or else it received the mean wear score of feathers when two or more wear classes were approximately equally represented in the area, as was common during molting. We assigned scores from 0 through 3 to remiges and rectrices based on the relative amounts of abrasion of barb tips of the longest primaries, the four innermost secondaries, and the rectrices, as illustrated in Willoughby (1991). Adding the scores of all plumage areas gave scores ranging from 0 (no appreciable wear anywhere) to 21 (heavily worn everywhere).

To test for repeatability of molt and wear scores by this method, EJW scored 20 study skins of various fringillid and emberizid finches twice, 7–11 days apart. The mean absolute difference between first and second scores was 0.8 for molt, and 1.3 for wear. Repeating the procedure a second time on five specimens with intermediate molt scores of 9–18, and seven specimens with intermediate wear scores of 6–11, yielded mean coefficients of variation of 10% and 11%, respectively.

Because they have more melanin pigment, males should experience less plumage wear than females (Burt 1986). Therefore, we compared monthly wear scores of males and females with the Mann-Whitney  $U$ -test, since these scores are ordinal rather than continuous. We treated each monthly sample as a random sampling of the population, independent of all other monthly samples. Because molt and wear scores of all samples  $>4$ , except those at the high end of the scoring scales, passed a Kolmogorov-Smirnov test for normality, we present means with standard errors to indicate central tendency and variability.

*Color comparisons.*—To assess seasonal changes in coloration, EJW scored a series of 10 male (2 AHY, 8 U) and 8 female (3 HY, 2 AHY, 3 U) skins in fresh plumage, collected September to December, and 13 male and 10 female skins (all AHY) in worn plumage, collected May through July, using the color standards in Kornerup and Wanscher (1978). Criteria for selecting a specimen for scoring were its being in typical adult plumage, the plumage area being free of obvious

smudges and stains, and feathers lying smoothly in their natural positions. We converted the Methuen tone designation A through F to numerical equivalent scores 6 through 1, respectively, and compared scores of hue, tone, and intensity between worn and fresh conditions with Mann-Whitney  $U$ -tests.

Reflectance spectroscopy permits more quantitative and precise color comparison than is possible when comparing with a limited series of color swatches (Smithe 1974). Differences among spectra may appear that are not distinguishable with color swatches, or not visible to the human eye, including differences in the ultraviolet portion of the spectrum. Therefore we obtained reflectance spectra from these same specimens using an Optronic Laboratories OL754 Portable High Accuracy UV-Visible Spectroradiometer with the OLIS-1000 Integrating Sphere reflectance/transmittance attachment, which integrates both diffuse and specular reflectances from the specimen. We measured spectral reflectance from the center of the yellow breast patch, from the center of the back where the yellowish color appears in males, and from the dorsal midline of the anterior back and nape. We exposed an area  $1 \times 1$  cm at the sample port, focusing the source beam on the center of that area, and masking surrounding areas with a white card having a  $1\text{-cm}^2$  cutout in the center. The instrument, calibrated for wavelength accuracy at 546.1 nm, recorded spectral reflectance at 5-nm intervals between 280 and 700 nm, and calculated percent reflectance based on known reflectance of a pressed polytetrafluoroethylene (Teflon<sup>®</sup>) standard. We extended the range into the ultraviolet (below 380 nm) to see whether there was significant reflection there, as has been observed for various species (Finger and Burkhardt 1994, Andersson 1996). Because of occasional discoloring or disarray, we did not scan all plumage areas on all specimens, which accounts for the various sample sizes presented in the results.

To check for precision of this method, we repeated scans of the breast (five scans), back (five scans), and nape (six scans) of a single specimen, removing and repositioning it at the sample port between each scan. These scans gave standard deviations (SD) at each 5-nm interval ranging from 0.144–2.87 (mean = 1.78) reflectance units. The mean coefficient of variation of all repeat measurements was 13.1%.

For each spectrum, we calculated the Commission Internationale de l'Éclairage (CIE) tristimulus values using the Optronics Laboratories optOLab spectroradiometer operating software. The tristimulus values, X, Y, and Z, represent the amounts of red, green, and blue light, respectively, from a standard source, which when combined produce the same color perception in a standard human observer. These values can be converted to the Munsell color notation system (Hardy 1936, American Society of Testing and Materials 1968, Ender 1990). From the tristimulus values, we calculated the corresponding Munsell color notation using Munsell Conversion, ver. 4.01 (Munsell Color, Gretag-Macbeth, New Windsor, New York).

We compared the mean reflectances of worn and



fresh plumages at all 5-nm wavelength intervals, and compared the CIE tristimulus values derived from the spectra within each sex using independent two-tailed *t*-tests, assuming unequal variances. Since our focus is primarily on the effects of plumage abrasion on coloration, and since males and females clearly differ in appearance, we did not perform statistical comparisons between the sexes.

*Feather micromorphology.*—During scoring, EJW noted a peculiar form of abrasion of yellow breast feathers in males, but not in females. This prompted us to look for micromorphological correlates of the peculiarity. EJW saved the approximately 0.3 body feathers per bird that separated from the study skins while scoring them for molt and plumage wear. To generate standardized samples for comparison, we used the available yellow feathers from near the center of the breast of five male and four female Lawrence's Goldfinches. For comparison with a species having the typical breast feather wear pattern, we used comparable feathers from five male Lesser Goldfinches (*Carduelis psaltria*), which were part of a separate investigation. Initially we examined and photographed some of these feathers under a dissecting microscope at 7–40 $\times$ . We then cleaned all the feathers by the method of Laybourne et al. (1992) and mounted each with the outer surface exposed on a 9.5-mm aluminum stub, using Avery "Spot-O-Glue" adhesive tabs (Avery Dennison, Commercial Products Division, Azusa, California). We sputter-coated these with gold-palladium in a Technics Hummer V sputter coater, or with gold in a Denton vacuum sputter coater.

We examined and photographed each specimen at various magnifications in a JEOL Model 5200 scanning electron microscope (SEM), at accelerating voltages of 5 or 10 kV, and a working distance of 20 mm.

We use the terminology for feather microstructure in Dove (1997). To compare measurements of the widths of the rachillae, we calculated mean rachilla width for a specimen measured at four points on the barbs near the tip of the feather, which we designated L1, L2, R1, and R2. These points were positioned as follows: L1 and R1 were on the terminal two barbs 300  $\mu$ m from the terminal bifurcation, and L2 and R2 were points on adjacent barbs intersected by straight lines perpendicular to the terminal barbs from points R1 and L1, respectively (Fig. 1). We compared the mean measurements of the widths of the rachillae with single-tailed independent *t*-tests, assuming unequal variances, and adjusted probabilities with a sequential Bonferroni procedure when comparing more than two groups simultaneously (Rice 1989, Sokal and Rohlf 1995).

## RESULTS

*Molt and plumage wear.*—AHY birds have one complete molt per year, beginning about the end of July and ending in late October or early November (Fig. 2), with no sign of the prealternate molt described as occurring dur-

ing March and April (Pyle et al. 1987, Pyle 1997, Davis 1999). Although we looked very carefully for this molt, we saw only a scattering of face and chin feathers in growth on 13 of 30 specimens collected during February and March, and on none of 42 collected during April and May. Such sparse replacement of feathers around the anterior face and chin in a minority of specimens probably represented adventitious replacement rather than traces of molting.

Replacement of remiges and rectrices was simultaneous with body molt, and followed the basic pattern common in passerines (Jenni and Winkler 1994). Most birds replaced rectrices quickly at the same time as remiges, but one bird in October and one in November were molting their tails after remex molt was nearly or quite complete.

Also beginning in late July, HY birds replaced all their body feathers, and some or all of their flight feathers (Fig. 2, Table 2), so that some birds then were indistinguishable from AHY, and could be identified as HY only by collectors' information on the labels. Of 11 specimens that had replaced some but not all primaries, 10 had molted in the eccentric pattern typical of passerines, starting at primaries 4, 5, or 6, and leaving variable numbers of juvenal proximal primaries (Jenni and Winkler 1994, Pyle et al. 1997). The remaining bird had replaced its proximal two primaries (1 and 2), thus having had an arrested descendant molt. Of six specimens that had molted some or all primaries and for which covert molt could be established, three had retained all juvenal primary coverts, and three had replaced them all. However, another bird that had retained all juvenal primaries had molted all its primary coverts. Of 19 specimens that had molted some or all secondaries, and for which molt of greater coverts was determined, 16 had molted all coverts, but three had retained various combinations of juvenal proximal coverts. One specimen had replaced all secondary coverts but had retained all juvenal secondaries.

The wear scores further indicate that no plumage replacement occurred during March and April, as plumage abrasion scores of AHY birds continued to increase throughout the spring (Fig. 2). Female specimens had accumulated significantly higher wear scores



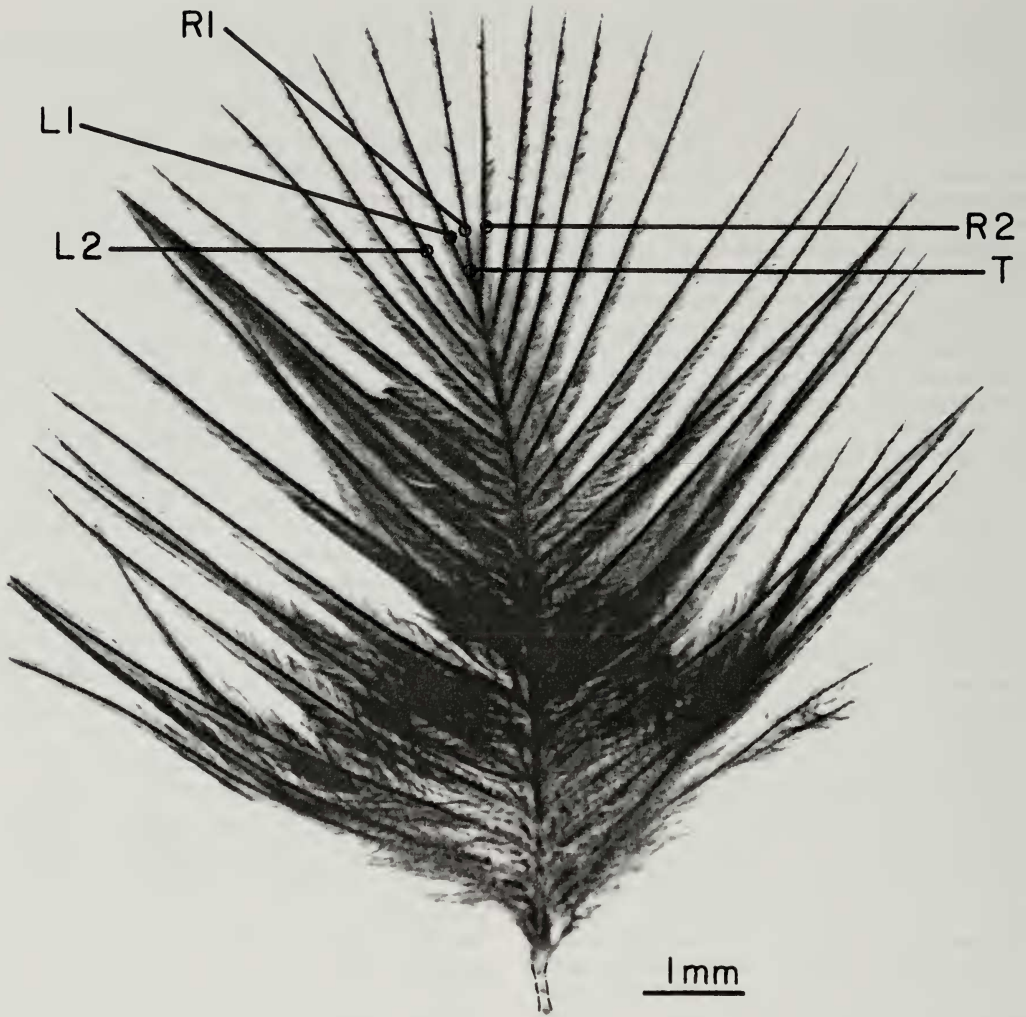


FIG. 1. Negative photographic image of a fresh yellow breast feather from a male Lesser Goldfinch (MVZ117922), to illustrate points on terminal barbs where widths of the rachillae were measured for micromorphological comparisons. Point T indicates the terminal bifurcation at the end of the rachis. Points L1 and R1 lie 300  $\mu\text{m}$  from T.

than males during June ( $P = 0.002$ ) and July ( $P = 0.029$ ). The difference is attributable to higher wear scores on the breast ( $P = 0.009$ ), throat ( $P = 0.022$ ), and crown ( $P = 0.003$ ), but not on the back, wings, or tail. Males are expected to have lower wear scores on crown and throat because of their black pigmentation (Burt 1986). Contrary to expectation, however, the yellow breast feathers of the males did not progress beyond a wear score of 2, while the surrounding gray feathers reached a uniformly maximum score of 3, as did both yellow and gray breast feathers of females.

The dissecting microscope revealed that the rachillae of these feathers abraded little at their tips, but the barbules broke off progressively from tip toward rachis, leaving longer portions of each barb denuded as time passed (Fig. 3b, top). Since our feather abrasion score was based on the relative length of barbs, wear scores stopped increasing once the slender, gray terminal segment, about 1 mm long, had broken off. At the same time, the yellow breast feathers of females, like those of the rest of the body, showed the usual pattern of wear in which the entire barb tip continued to

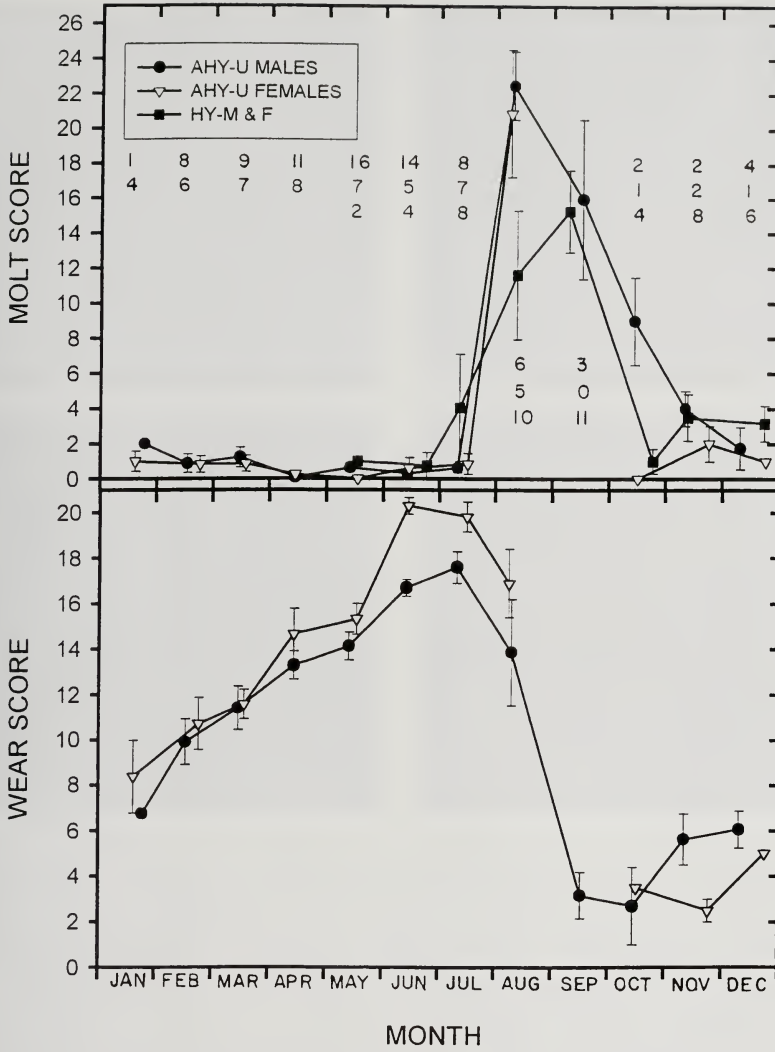


FIG. 2. Monthly molt and wear scores of Lawrence's Goldfinch specimens. Molt scores were elevated only between July and October, showing the period of the single annual molt from August to November, and the absence of molting in February through May before breeding. Mean scores ( $\pm 1$  SE) are plotted on the mean date of collection during the month. The numerals are sample sizes of AHY-U males, AHY-U females, and HY males and females, from top to bottom, respectively.

TABLE 2. Number of individuals (*n*) and percentage of sample of Lawrence's Goldfinch study skins identifiable as HY birds at the end of first prebasic molt, showing that juvenal remiges and rectrices may be replaced completely, partially, or not at all.

	All molted	Some molted	None molted
Primaries	3 (19), 16%	6 (19), 32%	10 (19), 53%
Secondaries	5 (19), 26%	12 (19), 63%	2 (19), 11%
Rectrices	16 (26), 62%	8 (26), 31%	2 (26), 8%

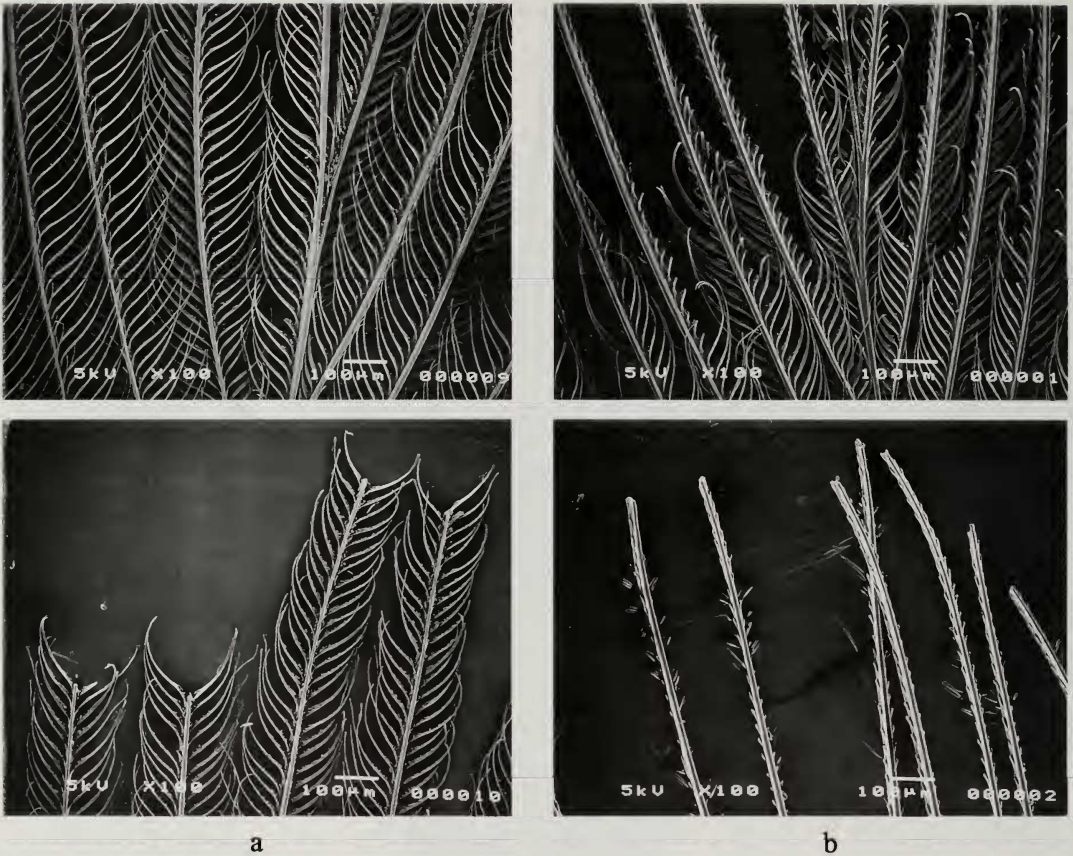


FIG. 3. Scanning electron photomicrographs of typical worn yellow breast feathers of female (a) and male (b) Lawrence's Goldfinches, showing differences in abrasion. The top micrographs show the terminal bifurcation of the rachis and the proximal parts of the terminal barbs, where measurements of rachillae were taken as in Fig. 1. The bottom micrographs show the distal ends of the same barbs. The female feather from USNM202998, 11 November, scored 2 (moderately worn), and shows how the tips of the barbs broke off to produce the characteristically irregular variations in length, while the barbules remained intact to the point where the barb had broken off. The male feather from LACM8469, 16 May, has all barbs of approximately equal length and scored 1 (lightly worn) because less than one third of their original lengths had been lost, despite being worn about eight months longer than the female feather. Unlike the female feather, barbules had broken off, leaving short rectangular stumps (b, bottom), but each barbule tended to break off gradually as shown by the partially abraded proximal barbules (b, top).

break away, progressively shortening each barb without denuding the remainder of its barbules (Fig. 3a, bottom).

*Micromorphological correlates of wear.*— Under the dissecting microscope we saw that the yellow breast feathers of all males had barbs richly pigmented with yellow carotenoids, with some brown pigment concentrated only around the tips of the barbules. With wear, these brownish barbules broke away, progressively denuding longer parts of the rachillae. In comparison, the yellow breast

feathers of the several hundred male American Goldfinches and Lesser Goldfinches we examined in similar studies showed the same progressive loss of barb tips seen in yellow breast feathers of the female Lawrence's Goldfinch. Breakage of barbules in males was concentrated near the tip of the feather, and occurred along most of the distal parts of each barb (Fig. 3b). Where each barbule had broken off was a short, rectangular stump (Fig. 3b). We could see no differences in shape or thickness of the bases of the barbules between



TABLE 3. Median (range) Methuen color scores,<sup>a</sup> with corresponding Methuen and Smithe color names, for adult Lawrence's Goldfinches in fresh and worn plumage, showing that worn males had more saturated breast color, and yellower, more saturated back color than fresh males, whereas worn and fresh females did not differ appreciably in this sample.

Sex, condition	Breast	Back	Nape
Males, fresh ( <i>n</i> = 10)	4C7 (4D7-4C8) (brass), 18 Orange Yellow	5F5 (4F4-5F7) (soot brown), 29 Brownish Olive	5F4 (5F3-5F6) (beaver), 29 Brownish Olive
Males, worn ( <i>n</i> = 13)	4C8 <sup>b</sup> (4D7-4C8) (dark yellow), 18 Orange Yellow	4F7 <sup>c</sup> (4F5-4E8) (olive brown), 29 Brownish Olive	5F4 (5F3-5E5) (beaver), 29 Brownish Olive
Females, fresh ( <i>n</i> = 8)	4D-E7 (4E6-4D8) (olive brown), 51 light Cit- rine	5F5.5 (5F5-5F8) (soot brown-Havana brown), 29 Brownish Olive	5F5.5 (5F5-6F8) <sup>d</sup> (soot brown-Havana brown), 119B Dark Drab
Females, worn ( <i>n</i> = 10)	4D8 (4E7-4D8) (olive brown), 51 light Cit- rine	5F5 (5F4-5F6) (soot brown), 29 Brownish Olive	5F6 (5F3-5F7) (Havana brown), 119B Dark Drab

<sup>a</sup> The first numeral denotes hue, increasing from yellow toward red; the capital letter denotes tone from A (lightest) to F (darkest), each letter denoting approximately twice the darkness of the preceding letter; and the last numeral denotes color saturation. Methuen color names from Kornerup and Wanscher (1978) are in parentheses. The approximate color match in Smithe (1975, 1981) is shown by the Smithe color number and name.

<sup>b</sup> Color saturation of worn plumage is significantly greater,  $P = 0.034$ .

<sup>c</sup> Hue is significantly more yellow,  $P = 0.018$ , and color saturation is significantly greater,  $P = 0.008$ , in worn plumage.

<sup>d</sup> The sample size is 7 due to missing feathers on nape of one specimen.

males and females that would explain the difference in wear. Furthermore, we noted that the barbules of males did not break off at any particular place, but abraded gradually from the barbule tip toward its base (Fig. 3b, upper). The rachilla of the male appeared noticeably thicker than those of the female.

Microscopic measurements of the widths of the rachillae of five males ( $13.2 \mu\text{m} \pm 1.3 \text{ SE}$ ) were significantly greater than those of four females ( $9.9 \mu\text{m} \pm 0.5 \text{ SE}$ ,  $P = 0.035$ ), and still wider than those of five male Lesser Goldfinches ( $8.6 \mu\text{m} \pm 0.3 \text{ SE}$ ,  $P = 0.015$ ). The rachillae of the female Lawrence's Goldfinches also were significantly wider than those of the male Lesser Goldfinches ( $P = 0.030$ ).

**Color changes.**—The series of male specimens we examined showed a yellow breast patch that appeared larger and brighter with the approach of summer. This change and the change in dorsal coloration of the males were well illustrated by Diane Pierce (National Geographic Society 1999:453). Our comparison of male specimens with color swatches in Kornerup and Wanscher (1978) and Smithe (1975, 1981) indicated that as plumage became more worn, the yellow center of the breast appeared significantly more saturated (Table 3), remaining a dark Orange Yellow. The center of the back showed a significant

increase in both yellowness and color saturation (Table 3), changing from near Olive Brown or Brownish Olive to a brighter, yellower color, approximating Citrine in several examples. Although the Methuen color scores did not reveal a statistically significant change of color on anterior back and nape, the general impression was of a reduction in tone and color intensity with wear, producing a lighter, grayer appearance in many but not all specimens. This was shown in the upper side of the range of observations, with a Methuen score of 5E5, in Table 3. Females changed much less, without significant changes in apparent color with wear (Table 3).

The apparent enlargement of the yellow area on the breast of the male resulted from abrasion of gray breast feathers surrounding the yellow patch. As these feathers became shorter, they uncovered the edges of the central patch of more durable yellow breast feathers. The increased yellow color of the center of the back resulted from brownish tips wearing off the feathers, exposing the yellow proximal parts of neighboring feathers. Discrete reflectances between 375 and 700 nm from the middle of the yellow breast of males did not change significantly with wear (Table 4), although the Munsell values calculated from the entire spectra indicated a shift toward the slightly greater apparent saturation seen in the

TABLE 4. Color analysis of reflectance spectra of center of breast ("breast"), center of back ("back"), and anterior back and nape ("nape"), showing that in Lawrence's Goldfinches, males get significantly more yellow on back and paler on nape, while females get significantly darker on breast and paler on back as plumage wears.

Sex	Plumage area, condition	n	Median wear score <sup>a</sup>	CIE tristimulus value, mean (SE)			Munsell notation, hue value/chroma
				X	Y	Z	
Male	Breast, fresh	9	1	37.7 (1.6)	33.6 (1.5)	5.2 (0.4)	9.23YR 6.30/11.00
Male	Breast, worn	10	1 <sup>b</sup>	36.0 (1.4)	31.8 (1.3)	4.6 (0.4)	8.98YR 6.15/11.15
				$P = 0.45$	$P = 0.36$	$P = 0.29$	
Male	Back, fresh	9	1	15.0 (0.5)	13.5 (0.5)	4.6 (0.2)	8.7YR 4.22/5.81
Male	Back, worn	11	3	19.0 (0.6)	17.2 (0.5)	4.8 (0.1)	9.38YR 4.70/6.81
				$P < 0.0001$	$P < 0.0001$	$P = 0.29$	
Male	Nape, fresh	10		15.3 (0.4)	13.8 (0.4)	5.1 (0.2)	8.83YR 4.27/5.51
Male	Nape, worn	11		16.9 (0.4)	15.4 (0.4)	5.8 (0.2)	9.05YR 4.48/5.55
				$P = 0.013$	$P = 0.008$	$P = 0.009$	
Female	Breast, fresh	8	1	33.0 (0.7)	29.9 (0.7)	7.2 (0.5)	9.20YR 5.99/8.89
Female	Breast, worn	10	2.5	29.4 (1.0)	26.5 (0.9)	5.5 (0.3)	9.30YR 5.68/9.06
				$P = 0.011$	$P = 0.009$	$P = 0.015$	
Female	Back, fresh	8	1	14.4 (0.3)	12.8 (0.3)	4.4 (0.1)	8.39YR 4.12/5.72
Female	Back, worn	9	3	18.4 (1.5)	16.7 (1.4)	6.0 (0.6)	8.71YR 4.64/5.96
				$P = 0.029$	$P = 0.026$	$P = 0.041$	
Female	Nape, fresh	8		15.0 (0.3)	13.4 (0.3)	4.8 (0.1)	8.53YR 4.21/5.66
Female	Nape, worn	9		15.6 (0.5)	14.1 (0.5)	5.0 (0.2)	8.74YR 4.30/5.66
				$P = 0.30$	$P = 0.25$	$P = 0.23$	

<sup>a</sup> The nape was not scored for wear, but was at least as worn as the back. Only wear scores of the yellow breast feathers are shown.

<sup>b</sup> Surrounding gray breast feathers scored 3, heavily worn.

Methuen color comparisons. The unworn breast reflected significantly more ultraviolet light than the worn feathers (290–370 nm,  $P = 0.033$  to  $P = 0.002$ ). The difference was small, and females showed nearly the same difference, so no sexual dichromatism was evident in the ultraviolet range (Fig. 4). In females, the unworn breast was significantly more reflective than the worn at all wavelengths between 295 and 700 nm ( $P = 0.020$  to  $P = 0.0002$ ), indicating that as the feathers abraded, the overall appearance became darker in value, but changed little in hue and chroma (Fig. 4, Table 4). This difference was not enough to be distinguishable with the Methuen color samples (Table 3).

The center of the back of worn males reflected significantly more between 490 and 700 nm (the green through red spectral regions) ( $P = 0.008$  to  $P < 0.0001$ ) than of unworn males. This contributed to its distinctly yellowish coloration (Fig. 4, Tables 3, 4). In contrast, wear of the backs of females produced a more variable effect, seen in the greater SE values in Fig. 4 and Table 4, and caused a small but significant increase of reflectance at wavelengths from 340 to 415 nm and 460 to 690 nm ( $P = 0.050$  to  $P = 0.009$ ).

Thus, color value and chroma both increased slightly (Table 4).

On the anterior back and nape of males, wear produced a significant increase of reflectance between 355 and 700 nm ( $P = 0.037$  to  $P = 0.0008$ ), appearing as a paler color, which contrasted more strongly with the black crown. In females, the color of this region did not change (Fig. 4, Tables 3, 4).

## DISCUSSION

Our results show that as the breeding season approached, sexual dichromatism became more pronounced: the male's Orange Yellow breast remained bright and expanded in area, and his Olive Brown dorsum became paler, contrasting more strongly with the black of the crown, and gained some yellow on the middle of the back. The female, in contrast, became duller on her breast and slightly paler dorsally. These color changes resulted from plumage abrasion, not from a prebreeding molt.

*Molting.*—Since we found no trace of a prealternate molt in the specimens we examined, we have to assume that the description of such a molt by others was based on an assumption that the color change prior to breed-

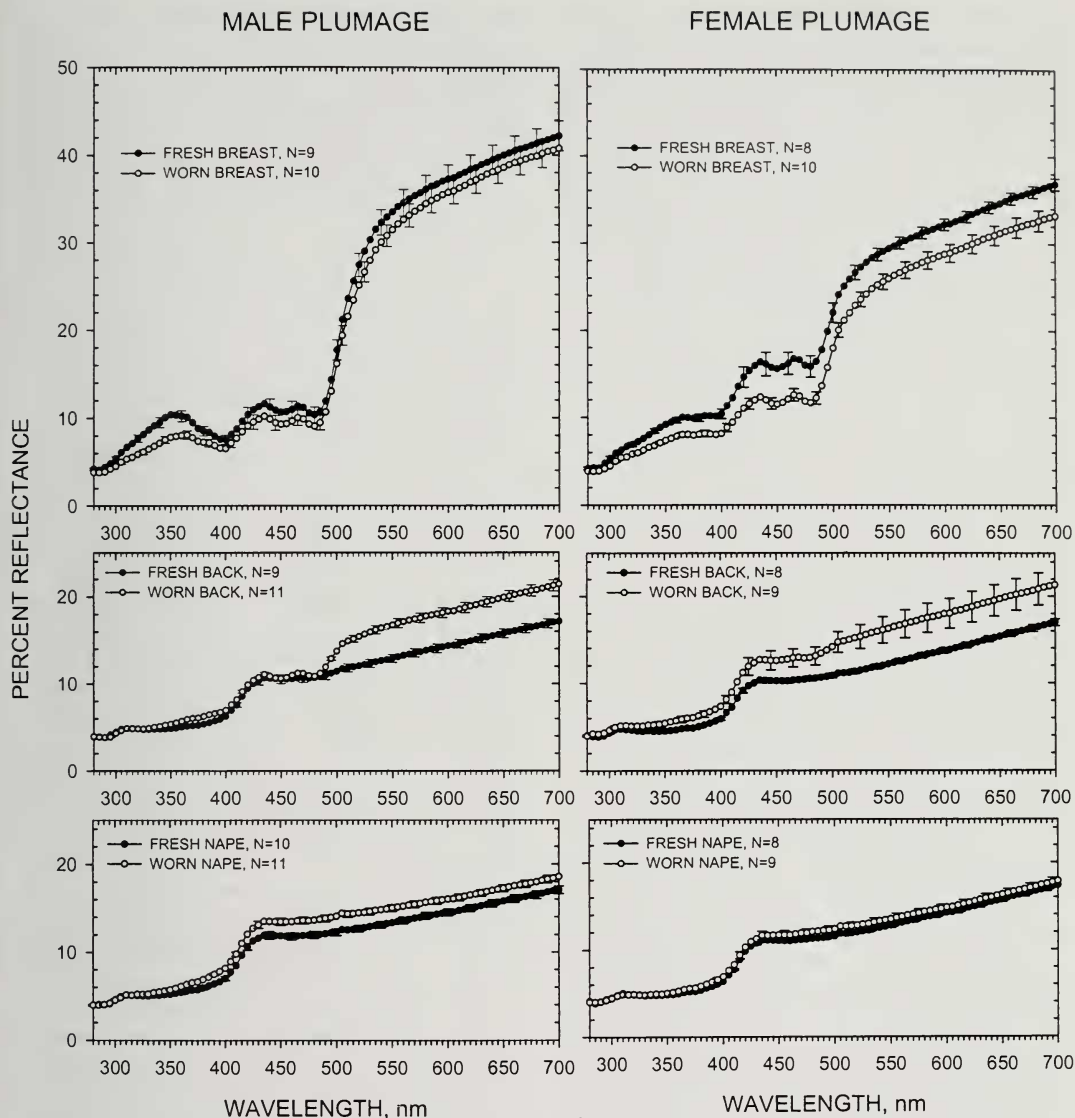


FIG. 4. Reflectance spectra constructed from mean reflectances of fresh and worn plumages at 5-nm intervals on breast, back, and nape of study skins of Lawrence's Goldfinch. Error bars ( $\pm 1$  SE) are staggered at 20-nm intervals for clarity. Worn male breasts reflected significantly less in the ultraviolet, but not in other regions of the spectrum, remaining bright yellow with wear, whereas worn female breasts reflected significantly less at nearly all wavelengths, becoming darker with wear. Worn male backs reflected significantly more in the green through red, becoming distinctly lighter and more yellow, whereas worn female backs reflected more in all visible wavelengths, so they became lighter but stayed nearly the same color. Worn male napes reflected significantly more in all visible wavelengths, becoming lighter, whereas female napes hardly changed with wear.

ing results from a molt. However, such a molt would be exceptional, because of the rarity of prebreeding molts within the *Carduelinae*. The American Goldfinch is the only cardueline species known to have an extensive prealternate molt that produces a change of color

(Middleton 1977, 1993). The American Goldfinch and Lesser Goldfinch are the only ones of 124 cardueline species reported unambiguously to have a prealternate molt that replaces most or all of the body feathers (Newton 1972, Clement et al. 1993, Middleton 1993,



Watt and Willoughby 1999). Therefore, finding such a molt in this or any related species would be unusual. Our results confirm that Lawrence's Goldfinch is comparable to the great majority of carduelines in having only one molt per year, a prebasic molt. When a cardueline does have a prealternate molt, it typically is of limited extent and does not change coloration. We advise investigators to examine specimens closely for evidence of molt, under a microscope when possible, to avoid coming to false conclusions. Such mistakes can distort the results of hypothesis testing procedures that rely on the accuracy of natural history data (e.g., studies of Rohwer and Butcher 1988, Butcher and Rohwer 1989, and Badyaev 1997a).

The great variation in the pattern of molting of primaries, secondaries, and their coverts during the first prebasic molt in our small sample is remarkable. Among species for which similar data are available, it appears closest to the Siskin (*Carduelis spinus*), which showed similar great variation among the small proportion of birds that had molted any primaries (Jenni and Winkler 1994). However, Lawrence's Goldfinch more frequently replaced primaries, and had even more variation, such as replacing juvenal primary coverts but not primaries.

*Morphological correlates of color enhancement.*—The peculiar thickness of the rachillae of the yellow breast feathers of males (Fig. 3) appears to be the reason that these feathers, by resisting wear and color loss, maintained their ability to provide a brightly colored patch that expanded in area with the approach of the breeding season. Morphological differences correlate with presence of carotenoid pigments in a variety of birds (Brush and Seifried 1968). The related Common Redpoll (*Carduelis flammea*) and Purple Finch (*Cardopacus purpureus*) have carotenoid-containing feathers that are modified such that they enhance exposure of the pigmented parts. This modification consists of a reduction in melanin pigmentation, elimination of barbules, and flattening of the barb, which increases the pigmented area exposed to view (Brush and Seifried 1968). The male Purple Finch, in particular, loses the barbules on its red crown feathers at the time its coloration brightens with approach of spring, while the barb tips wear

very little (Dwight 1900). These barbs become progressively denuded of their whitish barbules as the plumage becomes less hoary and brighter red in appearance (Dwight 1900). The breast feathers of the male Lawrence's Goldfinch therefore resemble the crown feathers of adult male Purple Finches in the way they wear.

*General comments.*—It is noteworthy that the three North American goldfinches and the Pine Siskin, judged in a recent analysis to be phylogenetically more closely related to each other than to any other member of the genus (Badyaev 1997b), demonstrate a full range of variation in sexual dichromatism and annual molt cycles. The Pine Siskin (*Carduelis pinus*), at one extreme, has no sexual dichromatism, and a single annual molt (Dawson 1997, Pyle et al. 1997). In the American Goldfinch, at the other extreme, males alternate between a dull, female-like nonbreeding plumage and a bright, highly sexually dichromatic breeding plumage through alternation of a complete prebasic molt and an extensive prealternate body molt (Middleton 1993). The Lesser Goldfinch is variable with respect to molting. It is sexually dichromatic and keeps the same appearance all year, but those of the Pacific coast states and Baja California have a single annual molt, whereas those of the interior states and the rest of Mexico have two complete molts per year (Watt and Willoughby 1999). The Lawrence's Goldfinch, as demonstrated here, is sexually dichromatic all year, but becomes more so during the breeding season, not by a molt, but by feather abrasion. These observations indicate that variations of sexual dichromatism and molting cycle are not phylogenetically constrained in this group, and suggest that such variations may have evolved quickly and repeatedly within different lines of descent. Because all four species have ranges that overlap in California and Baja California and except for Lawrence's Goldfinch, have extensive overlap of ranges elsewhere, they should be a fertile group for investigating the roles of ecological, physiological, and behavioral factors influencing the evolution of both sexual dichromatism and molting cycles.

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